Minimum epidermal conductance of Norway spruce (*Picea abies*) needles: influence of age and shoot position in the crown

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Minimum epidermal conductance (g_{min}) of *Picea abies* (L.) H. Karst. needles was estimated for various positions and age classes. The values of g_{min} showed a lognormal distribution. There were no universal trends in correlation between g_{min} and shoot position in the crown. The values of g_{min} increased significantly in the course of needle ageing. All sample series displayed high variability, which may be caused by differences in stomatal closure and/or in cuticular conductance *sensu stricto*.

Keywords: cuticle, epicuticular wax, minimum epidermal conductance, needle ageing, *Picea abies*

INTRODUCTION

Cuticular transpiration constitutes only a small part of water losses from conifer needles. However, in extreme conditions cuticular water loss may play an important role in the water economy of conifers. It has been shown that transpiration through the needle surface can determine the survival of conifers at the alpine timberline (Baig & Tranquillini 1974) or in polluted areas (Barnes & Davison 1988). Due to many methods-related difficulties in measuring the cuticular conductance of amphistomatal leaves or needles "minimum epidermal conductance" (g_{min}) is a more correct term to use when values are calculated from leaf weight-loss curves in desiccation experiments (van Gardingen *et al.* 1991). The value of g_{min} changes in time and is influenced by temperature and cuticle water content (Kerstiens 1994).

The values of g_{min} for conifer needles are closely related to the quantity and structure of epicuticular wax. Koppel and Heinsoo (1994) showed that removal of epicuticular wax from Norway spruce (*Picea abies* (L.) H. Karst.) needles can increase g_{min} by up to 44%. The quantity and structure of epicuticular wax of conifer needles has been widely investigated. Epicuticular wax on newly formed needles has a microcrystalline fine structure. With needle ageing wax degrades and forms fused tubes and platelets (e.g., Huttunen & Laine 1983, Ber-

madinger *et al.* 1988). At the same time g_{min} of older needles increases (Hadley & Smith 1994, Schreiber 1994).

Air pollution accelerates the rate of wax "ageing" (e.g., Crossley & Fowler 1986, Sauter & Voß 1986). Changes in epicuticular wax structure may be caused also by the micromechanical action of precipitation, and wind and dust particles (Günthardt-Goerg 1994). It has been shown that wax structure may vary on different needle sides of the same needle (Günthardt-Goerg 1994), or on the needles of the same age class, collected from different crown positions (Kim 1985). Unfavourable climatic conditions may also harm cuticle development and the layer of epicuticular wax of newly formed leaves. In tobacco (*Nicotiana tabacum* L.) the biosynthesis of epicuticular wax is affected by UV-radiation (Barnes *et al.* 1994). The influence of wind on cuticle development and g_{min} has been reported for several deciduous trees growing in upland hills (Hoad *et al.* 1994) and for conifers growing at timberline (Baig & Tranquillini 1976, van Gardingen *et al.* 1991).

In conifer species the values of measured g_{min} vary on a large scale even in experiments with one species (reviewed by Kerstiens 1996). At the same time the mean values of g_{min} for one species may show very high standard errors in one experiment(e.g., Hadley & Smith 1990, Koppel & Heinsoo 1994). This variability may cause problems when the values of g_{min} are used for modelling wintertime water loss from needles. The aim of this study was to analyse the spatial variability of minimum epidermal conductance within the crown of Norway spruce and to estimate changes in g_{min} during needle ageing.

MATERIAL AND METHODS

Sample trees

Shoots for investigation were collected from three approximately 70-year-old spruces growing in an open site close to the Vooremaa Ecological Station, Central Estonia. Two trees (Nr. 1 and 2) were used for studying the variability of g_{min} within the crown. The study was carried out on current-year shoots (C) and on two-year-old (C + 2) shoots in autumn 1995. The shoots were collected from the top (30 m),

middle (14 m) and bottom (2 m) of the crown, both from the northern and southern sides of the tree. Six shoots were sampled from distal and proximal branch parts for each height/year class. The branches were severed and taken to the laboratory in plastic bags.

One tree (Nr. 3) was used to study changes in g_{min} during needle ageing. One cohort of shoots (sprouting at the end of May 1985) was monitored through two and half years (from June 1985 until October 1987). In the same tree g_{min} of shoots was estimated for four previous year classes in spring before budbreak(marked as C + 1, C + 2, C + 3 and C + 4). For this, shoots were collected from the height levels of 6 m and 18 m (eastern side) as well as 2 m (eastern and western sides). Sample size was ten shoots per age class/ position.

Measurement of minimum epidermal conductance (g_{min})

The shoots were detached from the branch in the laboratory and the cut surface of the twig was covered with latex glue to prevent evaporation. The shoots were hung up in a closed room at dim light. Air humidity and temperature were measured with a ventilated Assmann psychrometer. Needle temperature was considered to be equal to air temperature. It was assumed that stomata were closed after 4 hours of desiccation. The values of g_{min} were calculated over the period 4–14 hours from the beginning of the experiment. Total needle surface area was estimated by the glass bead method (Thompson & Leyton 1971).

Minimum epidermal conductance was calculated as:

$$g_{min} = \Delta m/((\varsigma_{sat\ Tn} - \varsigma_{sat\ Ta} \times RH) \times t \times S),$$

where Δm is water loss in the period, ς_{sat} is the saturating water vapour concentration at a given needle (Tn) and air (Ta) temperature, RH is relative air humidity, t is the length of the period, and S is the total needle surface area. The surface area of needles was many times larger than that of the twig. Therefore the water loss through the twig bark was assumed to be negligible. For statistical analysis SAS System GLM procedure for classes was used.

RESULTS

Data distribution

Analysis of g_{min} demonstrated a lognormal data distribution. Therefore the geometric mean of non-transformed data was used instead of the arithmetic mean. For statistical analysis lognormal transformation of the data was used.

Spatial variability of g_{min} in the crown

Statistical analysis showed that there were no universal trends in correlation between shoot position in the crown and g_{min} (Table 1). In tree Nr. 1 shoots taken from the northern side of the tree had larger values of g_{min} compared to those taken from the southern side. In tree Nr. 2, the results were the opposite. The role of the quadrant was significant only for C-needles. Analysis of the joint effect of several factors did not reveal any general trends either.

The mean values of g_{min} for tree Nr. 1 are used to describe the behaviour of minimum conductivity in the tree crown (Fig. 1). The mean values of g_{min} for C-needles within the crown of this tree varied in the range 1.7–4.3×10^{-5} m s^{-1}. The values of g_{min} in C + 2 needles were always about twice as large.

Needle age and g_{min}

Minimum conductance of needles increased steadily during needle ageing (Fig. 2). According to statistical analysis, the largest differences in g_{min} occurred during the third growing period of needles. Differences between g_{min} of C + 1 and C + 2 as well as between C + 3 and C + 4 needles were not statistically significant. The distribution histograms of g_{min} showed a significantly higher variability in older age classes. The frequency class with the largest number of measurements was almost the same for all age groups. However, for older shoots the distribution curves extended towards higher g_{min} values (Fig. 3).

The study of g_{min} needles over two years demonstrated that g_{min} declined rapidly in the first weeks after budbreak. Afterwards g_{min} increased steadily with needle ageing. At the same time large fluctuations of g_{min} occurred against the background of this increase. For example, in April 1986, g_{min} was about twice as high as in March 1986. In May 1986, g_{min} dropped to the level of March (Fig. 4). The variability of g_{min} did not correlate with water vapour deficit calculated from air climate parameters of the laboratory.
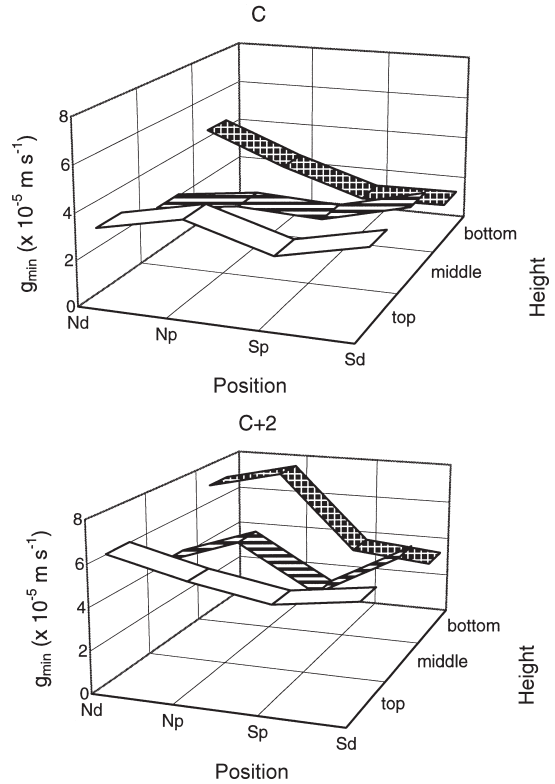

Fig. 1. Pattern of minimum epidermal conductance of C and C + 2 shoots in the crown of tree Nr. 1. Height: 2 m (bottom), 14 m (middle) and 30 m (top); position: northern distal (Nd), northern proximal (Np), southern proximal (Sp) and southern distal (Sd).

Table 1. Influence of various factors on g_{min} of trees Nr.1 and 2. C: current-year needles; C + 2: two-year-old needles. Quadrant: northern vs. southern side of the tree; distance: distal vs. proximal part of the branch; age: C *versus* C + 2 needles. *** = $p < 0.005$; ** = $p < 0.01$; n.s. = not significant.

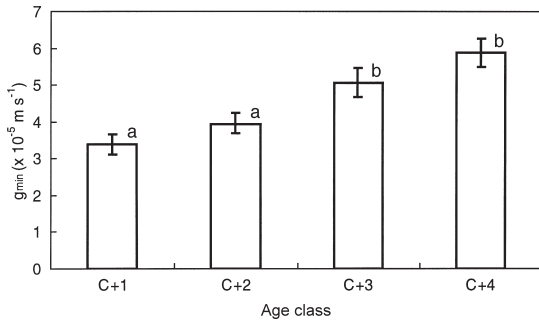|	Tree Nr. 1		Tree Nr. 2	
	C + 2	C	C + 2	C
Factors:				
Height	n.s.	n.s.	n.s.	***
Quadrant	***	***	n.s.	***
Position	n.s.	n.s.	**	***
Age	***		***	

Fig. 2. Changes in g_{min} during needle ageing in tree Nr. 3. Bars: ± S.E. ($n = 40$). Columns with different marks are statistically different ($p < 0.05$; Bonferroni *T*-test).

DISCUSSION

Baur (1997) showed that water permeability and organic solute mobility in nonstomatal plant cuticles are characterised by lognormal distribution. Normal distribution was found in cuticles when cuticular waxes were extracted. Thus lognormal distribution can be attributed to the presence of the wax layer. Epicuticular wax consists of a mix of different components with different water permeability. Considerable variation in its composition might cause the described permeability distribution. Our results demonstrated that the values of g_{min} in the desiccating amphistomatal needles of *Picea abies* are also characterised by lognormal distribution. However, the reasons of this distribution pattern are unclear. It may be caused partly by the above-described phenomenon, but an alternative/additional explanation can be suggested as well. It has been shown that evaporation from stomatal leaf surfaces includes a stomatal component (Kerstiens 1996). If the degree of stomatal closure differs for the shoots, the lognormal distribution of g_{min} is expected.

The values of g_{min} are supposed to depend on the quantity and structure of epicuticular wax (Schulze 1989, Turunen & Huttunen 1990). Epicuticular wax lost its original structure most rapidly in the top of the tree crown and on the adaxial surface of needles (Kim 1985, Günthardt-Goerg 1994). It is possible that such differences might cause changes in the minimum cuticular conductivity of needles occupying different positions in
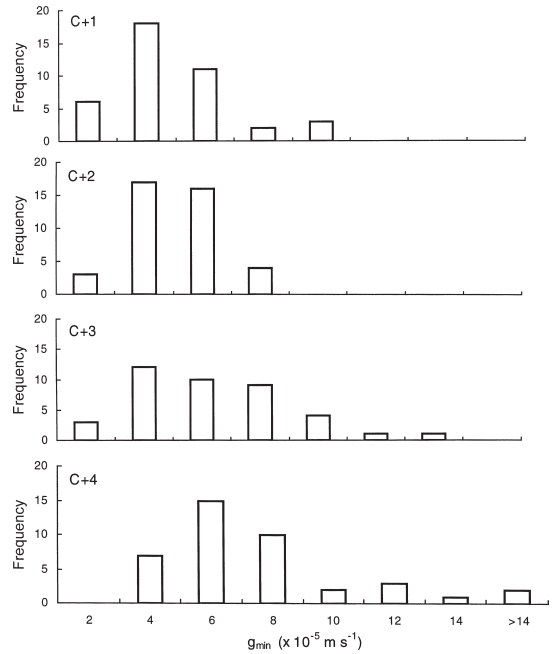

Fig. 3. Frequency distribution of g_{min} of various age classes ($n = 40$).

the crown. In treeline experiments, differences in cuticle thickness and g_{min} between wind-exposed and wind-protected shoots have been found (Baig & Tranquillini 1976, Hadley & Smith 1983). The amount of solar radiation and wind climate differ essentially for various heights and positions in the crown. However, we did not find any significant differences in g_{min} between shoots occupying different crown positions. Therefore, we conclude that microclimate differences within the crown do not influence g_{min}.

Permeability of the current year cuticles of *Picea abies* with respect to pentachlorophenol differs statistically from that of older cuticles (Schreiber 1994). In *P. engelmannii* Engelm. needles, g_{min} increased after the first wintering of needles in the Central Rocky Mountains, USA (Hadley & Smith 1994). At the same time there were no significant differences in g_{min} of older year classes. We found that g_{min} increased gradually with needle age until the fifth year at least. The largest differences in g_{min} were revealed between C + 2 and C + 3 shoots (Fig. 2). Different results might be explained by the more stable wax structure of *P. abies* or/and by milder climatic conditions.

The distribution of g_{min} values for different age class needles (Fig. 3) shows that only a relatively small proportion of older needles have lost their original capacity to minimize uncontrollable water loss during ageing. It has been claimed that one of the main causes of increase in g_{min} of older needles is the degradation of initial epicuticular wax structure during needle ageing (Huttunen 1994). On the other hand, g_{min} of older needles was significantly higher even if their wax layer was removed (Koppel & Heinsoo 1994). This indicates that besides changes in the amount and quality of wax, cuticle permeability or/and the number of dysfunctioning stomata may increase with needle ageing.

The influence of climate on g_{min} during needle ageing is yet unclear. Our investigation of the needles of one year class throughout two years showed a fast decline of g_{min} during the first weeks of growth (Fig. 4). This is most likely due to the presence of immature cuticle as well as additional evaporation through the twigs of a newly sprouted shoot. Conductance drops in the course of shoot maturation. In mature needles, g_{min} increases steadily for years with no significant differences between the seasons (Fig. 4). High variability of the calculated mean of g_{min} over many years is probably caused by different climatic conditions and/or most likely, by differences in stomatal closure. As has been found, permeability of the plant cuticle and hence g_{min} depends on temperature and humidity (Kerstiens 1994, Sowell *et al.* 1996). At the same time no correlation was found either between g_{min} on the one hand and room humidity or temperature on the other.

The minimum conductance of *Picea abies* needles, as calculated by a number of authors, varies in the range of $0.3–8.7 \times 10^{-5}$ m s^{-1} (Kerstiens 1996). There are several reports about large variations of g_{min} in one experiment. Hadley and Smith (1990) calculated the variation coefficient of g_{min} in *Abies lasiocarpa* (Hook.) Nutt. needles as 16%. The mean variation coefficient in our experiment over two years was 14.8%. At the same time the variation coefficient of the mean values of g_{min} measured throughout one year (January–December 1986) was 39.6%. Such high variability of g_{min} should be kept in mind when modelling wintertime water economy in conifers.
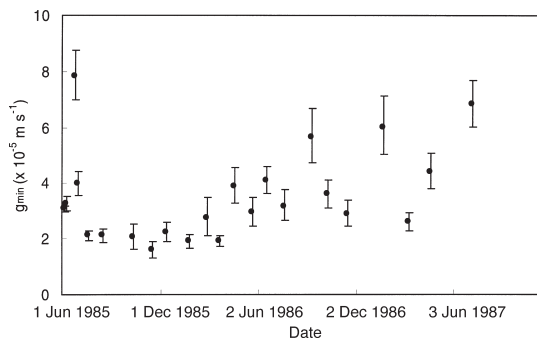

Fig. 4. Changes in g_{min} during two and half years after sprouting of the studied shoots. Bars: ± S.E.

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